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Diapause status of females affects attraction of male pear psylla, *Cacopsylla pyricola*, to volatiles from female-infested pear shoots

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Abstract

A companion study showed that male pear psylla, *Cacopsylla pyricola* (Förster) (Homoptera: Psyllidae) were attracted to volatiles from pear shoots infested with post-diapause females. The present study compared the behavioral response of males to diapause and post-diapause females. Assays were done using a Y-tube olfactometer. We collected male and female winterform psylla from pear orchards at regular intervals between late October (early diapause) and late February (post-diapause). Female-infested shoots were not attractive to males until the February samples, coinciding with ovarian maturation and onset of mating in the field. A second set of assays was done in which we manipulated diapause status in the laboratory either by exposing psylla to a long-day photoperiod or by treating insects with an insect growth regulator, fenoxycarb. In the photoperiod experiments, both short-day and long-day males preferentially selected long-day (post-diapause) females over short-day (diapause) females. Fenoxycarb-treated males preferred fenoxycarb-treated (post-diapause) females over untreated (diapause) females; untreated males showed no preferences. Results support observations made elsewhere that male winterform pear psylla perceive and are attracted to volatile odors associated with pear shoots infested with post-diapause females.

Introduction

Pear psylla, *Cacopsylla pyricola* (Förster) (Homoptera: Psyllidae), is a major pest of commercial pears throughout Europe and North America. The species exhibits a seasonal dimorphism, overwintering in the adult stage as a large, dark 'winterform', which is distinct from the smaller and lighter colored morphotype ('summerform') that occurs during the growing season. The dimorphism is controlled by photoperiod (Oldfield, 1970). The winterform morph overwinters in diapause, characterized by an absence of mating and immature ovaries. Diapause in central Washington ends apparently sometime in December (Krysan & Higbee, 1990; Horton et al., 1998) at which time cold field temperatures prevent mating and ovarian maturation. If winterforms are moved from the field beginning in late January and placed at warm temperatures in the laboratory, mating and ovarian maturation take place, irrespective of photoperiod in the laboratory (Krysan & Higbee, 1990; Horton et al., 1998). Under conditions in the study area, ovarian maturation and mating in the field begin in February, as temperatures begin to warm.

Post-diapause winterform females attract field-collected males in Y-tube olfactometers (Horton & Landolt, 2007). Assays tested female-infested pear shoots paired against uninfested pear shoots as the odor sources. The actual source of the volatiles that attracted the males in the assays was not determined (i.e., it is not clear whether the females or the female-infested shoots were the source of the attractants), but the results are at least consistent with the hypothesis that post-diapause female *C. pyricola* emit some sort of volatile sex attractant. Presence of sex pheromones has been shown or inferred to occur in a number of Homoptera, including mealybugs, aphids, scale insects, and whiteflies (Doane, 1966; Yin & Maschwitz, 1983; Millar et al., 2002; Campbell et al., 2003). Two studies (Soroker et al., 2004; Horton & Landolt, 2007) now present evidence for the possible existence of sex pheromones in Psyllidae, in both cases for species of *Cacopsylla*.

Here, we test whether diapause status of winterform females affects response of males to female-infested shoots

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in olfactometers. Behavioral studies and dissections of field-collected winterforms have shown that little or no mating occurs in diapausing psylla (Krysan & Higbee, 1990; Krysan, 1990b), and we hypothesized that diapausing females would not attract males in olfactometers. We collected male and female winterforms from the field at regular intervals to ascertain female attractiveness and male response. Our hypothesis is that females are unattractive to males until ovarian development in the field has begun. We also induced post-diapause development in winterforms by exposing diapausing insects to long-day photoperiods in the laboratory or to a juvenile hormone mimic (Krysan, 1990a; Horton et al., 1998), and compared diapausing and post-diapause females as paired sources of odors to males.

Materials and methods

Source of insects and plant material

Winterform pear psylla were collected from commercial pear orchards (cv. Bartlett) located near the USDA-ARS laboratory in Wapato, WA, USA (46°52′N, 120°47′W). The insects were collected using a beat tray and aspirator. Pear shoots were collected from the same orchards. We used reproductive shoots of first-year wood. Any dead leaves from the previous growing season still remaining on the shoots were removed before the shoots were used in the assays.

Y-tube olfactometer

The olfactometer is described fully in Horton & Landolt (2007). The apparatus was constructed of a 2.5-cm diameter glass tube 27 cm in length, having two arms (at 135° to one another) each 7 cm in length. The arms connect to treatment and control airflows, with the combined airflow vented out of the base of the Y-tube. Air (78% nitrogen, 21% oxygen) was metered through a carbon filter and humidity source, and into paired 1 l glass jars containing the odor sources to be compared. Airflow through each arm of the olfactometer was 50 ml min^{-1}. Males were assayed for choice. A single replicate consisted of 10 males, assayed one at a time. Males were allowed to exit singly from holding vials and enter the stem end of the olfactometer. Each male was then allowed 10 min to choose an arm of the Y-tube (choice defined to have occurred once the male contacted the end of an arm). Males not making a choice within a 10-min cut-off were discarded. For a given replicate, five males were assayed, the arms of the olfactometer were rotated 180°, and the second set of five males was assayed. Rate of air flow in each arm was measured before each assay, between the first and second groups of five males, and at the end of the replicate. Following each replicate of 10 males, the olfactometer was dismantled, washed thoroughly, and baked for 2 h at 150 °C. Assays were done at room temperature (22–25 °C) beneath fluorescent lighting.

Seasonality of female attractiveness

Studies were done between late October and late February in 2004–2005 and 2005–2006. Male and female winterform psylla were collected from the field at 3–4-week intervals for use in olfactometer trials, for a total of six collections made in both 2004–2005 and 2005–2006. For each of the 12 time intervals, 10 replicates (of 10 males per replicate) were assayed.

In 2004–2005, enough psylla to conduct 10 replicates within a sample week were collected 48 h preceding the first assay. The insects were then stored on pear shoots at 3 °C until they could be assayed. The 10 replicates per sample week were done within 2–5 days following the date of collection. Twenty-four hours before an assay, psylla were moved from storage into environmental chambers kept at temperature and photoperiod conditions similar to ambient field conditions. Sexes were separated and placed on pear shoots (collected 24 h earlier, and washed in tap water). Cut ends of the shoots were placed in tap water. Shoots were cut to approximately 10 cm in length. The females were stored in the same 1 l glass jars that were then used in the olfactometer trials. Ten females and three shoots were used per source jar; control jars had three uninfested shoots. Males to be assayed were kept on shoots in a second set of jars. Males and females were moved from the environmental chambers to room temperature 30–45 min before the assays were begun. Males were taken from the shoots and moved into the holding vials. Jars containing the females were carefully attached to the olfactometer, taking care to disturb the females as little as possible.

In 2005–2006, we modified methods to reduce handling of psylla and to eliminate the 3 °C storage intervals. For each sample week of 10 replicates, the insects were collected from the field 24 h before the assay and moved directly onto shoots. Thus, for each set of 10 replicates, we made 3–4 collections per week, depending upon how many replicates per day could be assayed. The shoots were collected at the same time as the psylla were collected. Females and shoots were placed in the jars that were to be used the following day in the assays. We increased the number of females in each jar from 10 (in 2004–2005) to 15, again using three shoots per jar. Control jars again each contained three shoots. Males were stored on shoots in a second set of glass jars. During the 24-h storage time between collection from field and running of the assay, jars containing females, males, or control shoots were stored at

24 °C and a L16:D8 photoperiod. Thus, in 2004–2005 the assayed insects were given 30–45 min at room temperature preceding the assay; in 2005–2006, the insects were given 24 h to acclimate to room temperatures. We saw substantial improvement in the assays the second year, as reflected by lowered numbers of unresponsive males (see Results).

On each collection date, 20 females from the field were dissected to determine ovarian development (an indicator of diapause status) and spermatophore numbers (to determine number of times that the female had mated). Methods are described elsewhere (Krysan & Higbee, 1990; Horton et al., 1998). Ovarian scores vary between 0 and 7, where 0 is immature and 7 is fully mature. The first mature egg is seen at stage 5; Krysan & Higbee (1990) considered stage 4 as defining the onset of post-diapause development.

Manipulation of diapause status in the laboratory

Diapausing winterform psylla were collected from the field in November, December, and early January of 2005–2006. Two sets of assays were done, using different methods to prompt post-diapause development.

Photoperiod. A long-day photoperiod was used to prompt post-diapause development (Horton et al., 1998). In early December, approximately 1000 psylla were collected from the field and separated by sex. We released the insects into four ventilated plastic buckets (20 l in size), with each bucket containing 250–300 psylla of one sex. We added 20–30 pear shoots into each bucket; cut ends of the shoots were kept in water. Two buckets (one containing females and one containing males) were placed in an environmental chamber at a L16:D8 photoperiod and temperature of 22 °C to prompt ovarian maturation. The other two buckets were placed in a second environmental chamber at a L10:D14 photoperiod and 22 °C to prevent or slow post-diapause development. At 2–3-day intervals, we dissected 5–10 females from the long-day chamber to determine ovarian development. Olfactometer tests were done once we began to obtain consistently females having ovarian scores of at least 5 (i.e., mature eggs present). Additional collections of psylla were made from the field in late December and early January, to conduct additional olfactometer trials in early January and mid-January, respectively. These extra assays were done to boost numbers of replicates up to the desired sample sizes (see below for sample sizes).

Once post-diapause females were obtained in the dissections, we began the behavioral assays. Diapause (short-day) and post-diapause (long-day) females were compared as the paired odor sources. Twenty-four hours before the assays, females were removed from the buckets and put into the glass jars that were to be connected to the olfactometer. We used 20 females and three pear shoots per jar. Shoots were collected from the field 24 h before each assay, and washed in tap water. Jars containing females and shoots were then stored in their respective short- or long-day environmental chamber for the 24-h settling period that preceded each assay. Males to be used in the assays were taken from buckets 30–45 min before the assays were conducted, and moved into holding vials. Fifteen replicates (of 10 males each) were done to assess the response of long-day males, and 15 replicates were done using short-day males. Order of replicates was randomized between short- and long-day males. At the end of each olfactometer run, 10 females were randomly taken from both the short-day jar and the long-day jar, and dissected to determine ovarian development.

Fenoxycarb. A second set of assays was done using an insect growth regulator to prompt post-diapause development. Fenoxycarb (Comply 25% WP; Ciba, Greensboro, NC, USA) was diluted to 0.5 g of product per 500 ml of water, and misted onto the inside surface of an empty 1 l glass jar. The sides were misted thoroughly (approximately 5 ml of solution). Once the product had dried, diapausing field-collected winterform psylla previously separated by sex were added to the jar and allowed to wander across the treated surface for 3 h. At the end of 3 h, females were moved onto untreated shoots in clean 1 l glass jars. The jars were those to be used in the olfactometer trials. Each jar contained 20 females and three shoots. Males were moved into ventilated 135 ml plastic vials, each containing three pear shoots. Control insects were treated the same as the insects that were exposed to fenoxycarb, except that the sides of the treatment jars were misted with tap water rather than with fenoxycarb. Treated and untreated insects were then moved to environmental chambers set at a L10:D14 photoperiod and temperature of 20 °C. The short-day conditions were used to maintain diapause in the control psylla; fenoxycarb-treated females mature their ovaries even under short-day conditions (Krysan, 1990a; Horton et al., 1998). We allowed 6–8 days for the fenoxycarb-treated females to mature their ovaries (Horton et al., 1998). Treated females (post-diapause) and untreated females (diapause) were compared as paired odor sources. We assayed both treated and untreated males, with replicates of the two types of males done in random order. We had 20 replicates (of 10 males each) for each type of male. Assays were done between early November and late December in 2005. Ten females randomly taken from each jar were dissected following each assay to determine ovarian development.

Statistical tests

Mean numbers of psylla entering the treatment arm of the Y-tube was compared to numbers entering the opposite

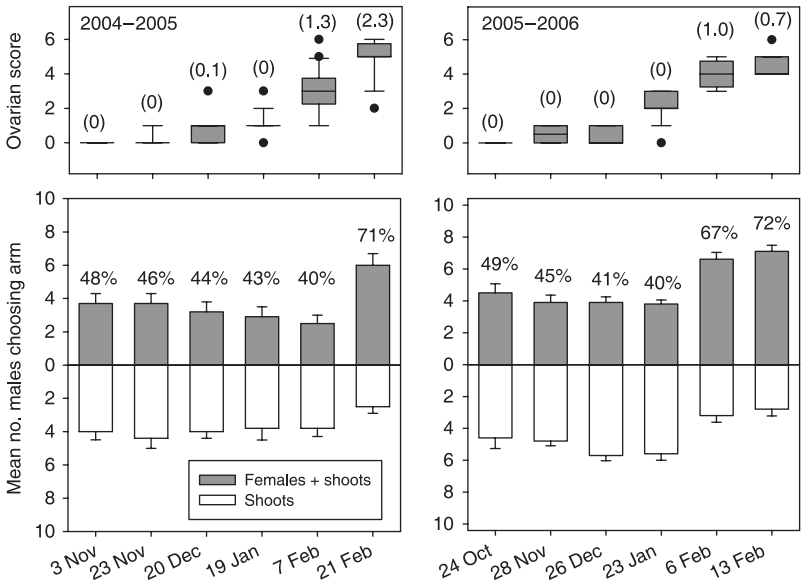

Figure 1 Seasonality of attractiveness. Upper panels: box plots showing ovarian scores in dissected females (n = 20 females per sample). Boxes depict 25th and 75th percentiles, horizontal line within box shows median, error bars show 10th and 90th percentiles, and filled circles depict outlying points. Numbers in parentheses show spermatophores per female. Bottom panels: mean (+ SEM) number of males choosing females + shoots (gray fill) vs. numbers choosing uninfested shoots (no fill). Numerals indicate percentage of males choosing the females + shoots treatment. Mean number of males choosing the female-infested shoots was significantly higher than numbers choosing the uninfested shoots in the 21 February, 2005 sample (paired sample t-test; t = 3.4, d.f. = 9, P = 0.009), the 6 February, 2006 sample (t = 4.1, d.f. = 9, P = 0.003), and the 13 February, 2006 sample (t = 5.5, d.f. = 9, P = 0.0004). There was a statistically significant (P<0.05) preference for the uninfested shoots in the 26 December, 2005 and 23 January, 2006 samples (paired-sample t-test and signed ranks test). Statistical tests for all remaining dates were all non-significant (P>0.05).

arm using a paired-sample t-test or a signed ranks test; the latter test was used if distribution assumptions for the t-test were not met (Horton & Landolt, 2007). The analyses were done in PROC TTEST or PROC UNIVARIATE of SAS (SAS Institute, 2001). Distribution assumptions for the paired-sample t-test were assessed using the Shapiro-Wilk statistic provided in PROC UNIVARIATE (SAS Institute, 2001).

Results

Seasonality of female attractiveness

In both years, male winterforms did not show a preference for female-infested shoots until the early to mid-February samples (bottom panels of Figure 1). The bars in the lower panels of Figure 1 show mean numbers of males choosing either the female-infested shoots (gray fill) or uninfested shoots (no fill). Each bar is a mean of 10 replicates. The gray and white fills sum to 10 if all males in each replicate made a choice. A larger percentage of males made a choice in the 2005–2006 assays than the 2004–2005 assays (Figure 1). Percentages of males choosing the female-infested shoots were in the low to high 40 s except for samples taken in February. There was a significant preference for the female-side of the olfactometer in the 21 February 2005 sample and in both the 6 February and 13 February 2006 samples (Figure 1). The study ended both years with the onset of pest sprays in the orchards following the final sample each February. In both years, there was evidence on some dates that males actually preferred the uninfested shoots (shown by percentages in the low 40 s), particularly on those dates immediately preceding samples in which female-infested shoots had become attractive (Figure 1). Indeed, there was statistical evidence that males preferred the uninfested shoots in the December 2005 and January 2006 samples (see P-statistics in Figure 1).

Box plots are shown in the upper panels of Figure 1 to illustrate ovarian scores in dissected females. Numbers in parentheses summarize mean numbers of spermatophores per female, and show that virtually no mating occurred until February both years. Winterform females became attractive to males in olfactometer tests as mature eggs were just beginning to form in field-collected insects (= ovarian scores of 5).

Manipulation of diapause status in the laboratory

Photoperiod. Both long- and short-day males significantly preferred long-day (post-diapause) females vs. short-day

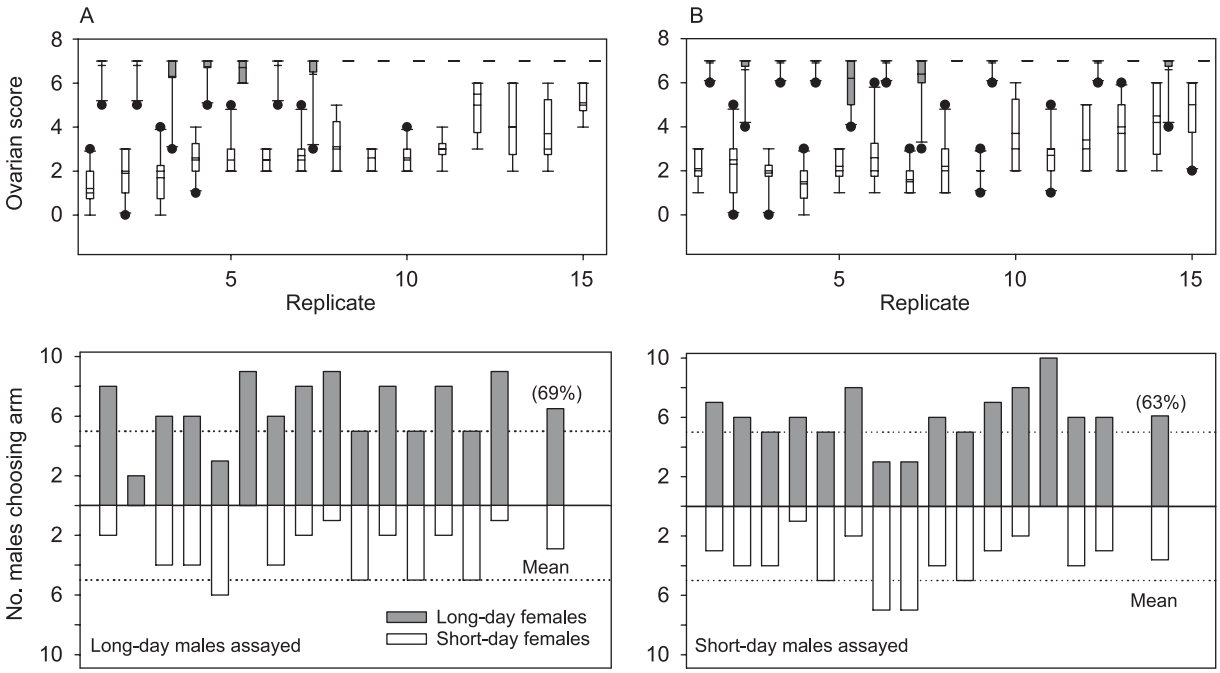

Figure 2 Photoperiod study; long-day (panel A) or short-day (panel B) males assayed. Upper panels: box plots showing ovarian scores of dissected females for short-day (no fill) and long-day (gray fill) treatments (n = 10 females per sample). Boxes depict 25th and 75th percentiles, horizontal lines within box show median and mean, error bars show 10th and 90th percentiles, and filled circles depict outlying points. Boxes along the X-axis are in same sequence as order of replicates: replicates 1–4 (late December 2005), replicates 5–12 (early January 2006), and replicates 13–15 (mid-January 2006). Lower panels: numbers of males within each replicate choosing long-day females (gray fill) when paired with short-day females (white fill); each odor source also included three pear shoots. The 15 bars (replicates) are shown in same sequence as order of replicates and associated ovarian score data (in the upper panel). Each bar based upon 10 males, minus those males not making a choice. The rightmost bar in lower panel shows means calculated from the 15 replicates. Mean number of males choosing long-day females was significantly higher than numbers choosing short-day females in both assays (long-day males: t = 3.9, d.f. = 14, P = 0.002; short-day males: t = 2.6, d.f. = 14, P = 0.02).

(diapause) females (bottom panels of Figure 2). Each bar in the bottom panels shows the results for one replicate. The two fills in a given bar sum to 10 if all males in that replicate made a choice. Mean numbers of males choosing each arm are shown in the rightmost bar of both figures. Box plots (upper panels in Figure 2) show ovarian scores in females from each replicate. Horizontal lines without boxes (e.g., replicates 8–15 in Figure 2A) indicate that 100% of females had ovarian scores of 7. We had good separation in ovarian scores of short- vs. long-day females in both sets of assays (Figure 2).

Fenoxycarb. Males that were treated with fenoxycarb preferred fenoxycarb-treated (i.e., post-diapause) vs. untreated (i.e., diapause) females (bottom panel of Figure 3A); untreated males showed no preferences (Figure 3B). In both sets of assays, a substantial percentage of untreated females unexpectedly contained mature eggs (ovarian scores of at least 5; white-filled box plots, upper panels of Figure 3), so treatment differences in physiological age of females were considerably less pronounced in this study than in the assays done using photoperiod to prompt ovarian development. Overlap in ovarian scores of treated and untreated females was particularly evident in the later replicates, for unknown reasons.

Discussion

Pear psylla, *C. pyricola*, overwinters in diapause, characterized by absence of mating and lack of ovarian maturation (Krysan & Higbee, 1990; Horton et al., 1998). The lack of mating appears to be a specific part of the diapause syndrome (Krysan, 1990b; Krysan & Higbee, 1990). Thus, almost no mating occurs in winterform pear psylla until February, even though temperatures at the beginning of the generation in autumn are easily warm enough to allow mating, and despite the observation that newly emerged males of the winterform generation have active sperm in

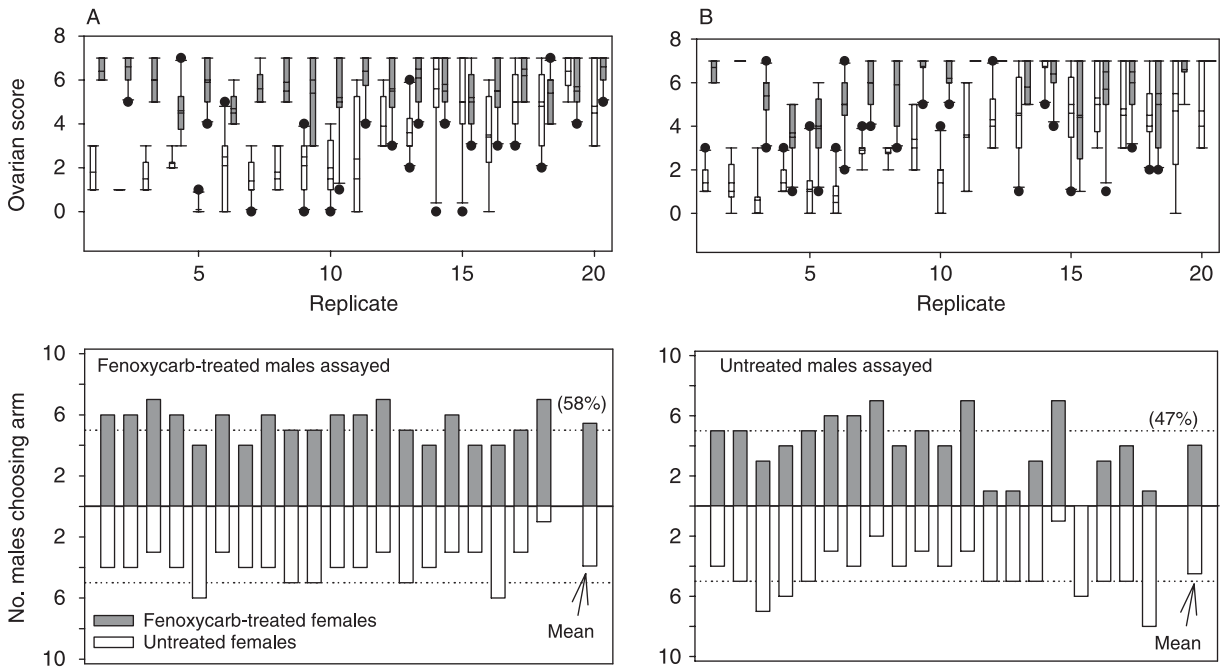

Figure 3 Fenoxycarb study; treated (panel A) or untreated (panel B) males assayed. Upper panels: box plots showing ovarian scores for untreated (no fill) and fenoxycarb-treated (gray fill) females (n = 10 females per sample). Boxes depict 25th and 75th percentiles, horizontal lines within box show median and mean, error bars show 10th and 90th percentiles, and filled circles depict outlying points. Boxes along the X-axis are in same sequence as order of replicates; assays were done between early November and early December. Lower panels: numbers of males within each replicate choosing fenoxycarb-treated females (gray fill) when paired with untreated females (no fill); each odor source also included three pear shoots. The 20 bars (replicates) are shown in same sequence as order of replicates and associated ovarian score data (in the upper panel). Each bar based upon 10 males, minus those males not making a choice. The rightmost bar in lower panel shows means calculated from the 20 replicates. Mean number of males choosing the treated females was significantly higher than numbers choosing the untreated females in assays with treated males ($t = 3.5$, d.f. = 19, $P = 0.002$) but not in assays with untreated males ($t = -0.6$, d.f. = 19, $P = 0.58$).

the testes and seminal vesicles (Krysan & Higbee, 1990). Indeed, behavioral tests in small Petri dishes have shown that diapausing male pear psylla will attempt to mate winterform females, but the males are rejected (Krysan, 1990b). Only post-diapause males are in general allowed by females to copulate (Krysan, 1990b).

Even though male psylla will attempt to mate diapausing females if the two sexes are together in small arenas (Krysan, 1990b), the studies here showed that diapausing females fail to attract males in olfactometers. These somewhat contradictory results suggest that male pear psylla use more than a single type of cue to locate females for mating. Vision apparently has a role in short-distance interactions, as suggested by the behavioral studies of Krysan (1990b) and the brief observations of Cook (1963). Diapausing females appear to be visually attractive to male pear psylla in small Petri dish assays. Acoustic signaling between the sexes is also important for mediating short-distance encounters in species of Psyllidae (Tishechkin, 1989; Percy, 2005), although there is as yet no evidence for *C. pyricola* that this psyllid uses acoustic cues in mediating sexual encounters.

Results reported here and in Horton & Landolt (2007) suggest that post-diapause winterform *C. pyricola* also use olfactory cues in sexual encounters. Soroker et al. (2004) showed that male summerform psylla, *Cacopsylla bidens* (Šulc), a species closely related to *C. pyricola*, were attracted to pear foliage infested with female *C. bidens*. The studies by Soroker et al. (2004) with *C. bidens*, and our research with *C. pyricola* (Horton & Landolt, 2007; herein) appear to be the only published accounts suggesting that any species within the Psyllidae emit volatile sex attractants, despite numerous examples for other Homoptera (e.g., Einhorn et al., 1998 for Diaspididae; Lanier et al., 1989 for Magarodidae; Millar et al., 2002 for Pseudococcidae; Campbell et al., 2003 for Aphididae).

If attraction by male winterforms to females in olfactometers was due to volatile sex attractants being emitted by females, then volatile production by winterform *C. pyricola* appears to be regulated in part by diapause. That is,

diapausing females failed to attract males in the phenological studies (Figure 1), in the photoperiod studies (Figure 2), and in the fenoxycarb assays (Figure 3). In contrast, post-diapause females, whether obtained from the field or induced in the laboratory to mature their ovaries, were attractive to males in the olfactometer trials. In sum, if the attractant that mediated male behavior was indeed emitted by the female psylla, then diapause in *C. pyricola* affects several physiological and behavioral processes in this species, including apparently female production of sex attractants. Diapause is known to affect pheromone production or response to pheromones in other insect species (Borden, 1977; Tauber et al., 1986), and results reported here for *C. pyricola* may provide an additional example.

The assays in which fenoxycarb was used to prompt ovarian development in diapausing females were not as consistent in showing male attraction to females as the assays in which long-day photoperiod was used to prompt post-diapause development (compare Figures 2 and 3). Indeed, in the fenoxycarb trials, untreated males showed no preference for treated females, while treated males exhibited a significant preference for treated females. At least two explanations can be proposed for the lack of preference by untreated males for fenoxycarb-treated females: (i) both fenoxycarb-treated and control females were emitting attractants; or (ii) treated females only emitted attractants, but untreated males failed to respond. Ovarian scores in control and treatment females showed extensive overlap in the fenoxycarb trials (Figure 3, upper panels), unlike what was obtained in the photoperiod trials (Figure 2, upper panels), so it is possible that both treated and untreated females were emitting attractants. The second explanation (i.e., that untreated males failed to respond to attractive females) seems unlikely, as diapausing males are apparently both physiologically and behaviorally ready to mate (Krysan & Higbee, 1990; Krysan, 1990b). Moreover, our photoperiod trials (Figure 2) showed that short-day males were attracted to long-day females, suggesting that diapause males both perceive and are attracted to volatile odors from post-diapause females.

Effective use of volatile sex attractants in integrated pest management programs requires knowledge of the target insect's sexual biology (Millar et al., 2002). In pear psylla, we have shown here and elsewhere (Horton & Landolt, 2007) that odors from post-diapause female psylla in association with pear shoots attract male winterform psylla. Attractiveness had a pronounced seasonality, with field-collected females failing to attract field-collected males until ovaries had begun to mature in February (Figure 1). Thus, if we are eventually to use volatile sex attractants in integrated pest management programs for pear psylla, we must carefully consider when (i.e., what time of year) the compounds are to be used. Additional study should be done to determine unequivocally the source of the volatiles (i.e., the female or the pear shoots). Assays should also be done to assess whether males of the summerform generation use volatile attractants to locate females (Soroker et al., 2004). Both objectives are currently being addressed.

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